H I L G A R D I A

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOL. 20 AUGUST, 1950 No. 7

MULTIPLE VIRUSES OF TOMATO INDUCING FRUIT MALFORMATION AND LEAF SYMPTOMS[1]

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DURING 1938 a serious outbreak of a peculiar disease on tomato plants was prevalent in the Byron and Brentwood districts of the northern San Joaquin Valley. At Byron approximately 95 per cent of the plants were diseased in a 96-acre field, and in other fields inspected 55 per cent were infected. Near Brentwood certain fields showed a lower percentage of infected plants. The progress of the disease was followed throughout the autumn.

Doolittle (1936, 1941)[3] was the first to report that tomato plants infected with the multiple viruses of tomato mosaic or tobacco mosaic and common cucumber mosaic bore fruits, which were deeply ridged, and when small showed pointed protuberances at the blossom end. The blossoms were commonly malformed and abortive. This disease occurred in greenhouse tomatoes in Ohio and Colorado. In Ohio, the common-cucumber-virus infection was traced to aphids evidently carrying the cucumber-mosaic virus from a nearby field of muskmelons, and in Colorado it apparently originated on cucumbers in another section of the greenhouse.

This paper deals mainly with an outbreak of the virus complex of western-cucumber and ordinary-tobacco-mosaic viruses on tomatoes in the northern San Joaquin Valley. Studies were made on the distribution and symptoms of the disease, on the effects of the multiple viruses on the flowers and fruit, and on the separation of the viruses in the virus complex. Studies were made on the aphid vectors of the western-cucumber-mosaic virus, and are herein reported. Further experiments were conducted, and are reported, with the multiple virus infections of celery calico and ordinary tobacco mosaic, and of common cucumber and ordinary tobacco mosaic.

MATERIALS AND METHODS

The source of western-cucumber-mosaic virus was naturally infected tomato plants obtained from fields at Byron and near Brentwood. The original source of the celery-calico virus was naturally infected celery obtained near Milpitas in the Santa Clara Valley. Common-cucumber-mosaic virus was kindly sent to me by James Johnson, University of Wisconsin. The method

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[3] See "Literature Cited" for citations referred to in text by author and date.

of mechanical inoculation used is that described by Rawlins and Tompkins (1936). Tomato plants of the Marglobe variety grown from seeds were used in all experiments. Checks on control plants of the same lots were used in all inoculation experiments. The Marglobe variety of tomato was selected because of the uniform shape of the slightly flattened, globe-shaped fruits.

MULTIPLE VIRUSES OF WESTERN CUCUMBER AND ORDINARY TOBACCO MOSAICS

Symptoms on Naturally Infected Tomato Plants. The symptoms on tomato plants naturally infected with western-cucumber and ordinary-tobacco-mosaic viruses were variable, owing probably to differences in environmental conditions associated with time of planting and infection. The plants in the field at Byron were severely stunted, from one and one-half to two feet tall, with upright stems. The infected plants made a bushy, compact growth, with very short internodes. Near Brentwood less dwarfing of infected plants occurred. One noticeable characteristic of the disease at Byron was the shoestring or filiform leaves on the plants. The few plants which did not exhibit filiform leaves were invariably mottled. The younger leaflets were thick, curled, and distorted with a pronounced yellowing along the veins. The older leaflets were rolled up at the margins and with yellowish-green mottling. Many of the leaves, however, were greenish purple along the veins and lower surface of the leaflets.

At Byron few fruits were set, were small, and failed to ripen normally. Near Brentwood, however, much fruit was set and was severely malformed. The most striking characteristic of the disease was the malformed fruit. Some of the fruit showed pointed protuberances at the blossom end (plate 1); doubling (plates 2, 3, *D*); tripling (plate 2, *A*, *B*, *C*); furrows (plate 2, *E*); furrows and protuberances (plate 2, *F*); ridges (plate 3, *A*); ridges and protuberances (plate 3, *F*); projections (plate 3, *B*) protuberances (plate 3, *C*); and small fruits telescoped in a large fruit (plate 3, *E*).

SEPARATION OF MULTIPLE VIRUSES

By Heat Treatment. An attempt was made to separate the viruses of western cucumber and ordinary tobacco mosaics which cause the disease. Since the thermal inactivation of the western-cucumber-mosaic virus is 65° C, while that of the ordinary-tobacco-mosaic virus is 90° to 95° C, a method of separating the two viruses was available. Accordingly, one portion of the expressed sap from six naturally infected tomato plants from Byron and near Brentwood was heated to 83° C for 11 minutes (allowing one minute for the heat to penetrate the glass test tube), then inoculated in sets of healthy tomato plants and *Nicotiana glutinosa;* while the unheated virus extract was inoculated in healthy tomato seedlings. The tomato plants inoculated with the heated virus extract were not affected, but *Nicotiana glutinosa* developed local lesions on the inoculated leaves. Tomato seedlings inoculated with the unheated virus extract developed typical symptoms of western cucumber mosaic. The type of infection of the tobacco-mosaic virus on *N.*

glutinosa was local, while that of western cucumber mosaic was systemic. This experiment (table 1) demonstrates that two separable viruses were contained in the original extract. It is evident that each of the six tomato plants was naturally infected with western-cucumber-mosaic and tobacco-mosaic viruses.

TABLE 1

SEPARATION OF WESTERN-CUCUMBER AND ORDINARY-TOBACCO-MOSAIC VIRUSES IN EXTRACTED JUICE FROM NATURALLY INFECTED TOMATO PLANTS BY HEAT TREATMENT AT 83° C

District	Virus extract from tomato plants	Host plants	Number inoculated	Number infected	Type of infection	Symptoms
Byron	Test 1, unheated	Tomatoes	10	8	Systemic	Filiform leaves, western cucumber mosaic
	Test 1, heated ...	Tomatoes	10	0	.....	.....
	Test 1, heated ...	*Nicotiana glutinosa*	5	5	Local	Local lesions, tobacco mosaic
	Test 2, unheated	Tomatoes	5	4	Systemic	Filiform leaves, western cucumber mosaic
	Test 2, heated ...	Tomatoes	5	0	.....	.....
	Test 2, heated ...	*N. glutinosa*	5	5	Local	Local lesions, tobacco mosaic
	Test 3, unheated	Tomatoes...	3	3	Systemic	Filiform leaves, western cucumber mosaic
	Test 3, heated ...	Tomatoes...	3	0	.....	.....
	Test 3, heated ...	*N. glutinosa*	3	3	Local	Local lesions, tobacco mosaic
	Test 4, unheated	Tomatoes...	3	3	Systemic	Filiform leaves, western cucumber mosaic
	Test 4, heated ...	Tomatoes...	3	0	.....	.....
	Test 4, heated ...	*N. glutinosa*	3	0	Local	Local lesions, tobacco mosaic
Brentwood	Test 5, unheated	Tomatoes...	6	6	Systemic	Filiform leaves, western cucumber mosaic
	Test 5, heated ...	Tomatoes...	6	0	.....	.....
	Test 5, heated ...	*N. glutinosa*	6	6	Local	Local lesions, tobacco mosaic
	Test 6, unheated	Tomatoes...	3	3	Systemic	Filiform leaves, western cucumber mosaic
	Test 6, heated ...	Tomatoes...	3	0	.....	.....
	Test 6, heated ...	*N. glutinosa*	3	3	Local	Local lesions, tobacco mosaic

By Filter Plants. The viruses of western cucumber and tobacco mosaics were separated by inoculating White Spine cucumbers (*Cucumis sativus*), Zucchini squash (*Cucurbita pepo*), and *Nicotiana glutinosa* with the expressed juice of naturally infected tomato plants. In each test, the juice of one tomato plant was applied to sets of five each of the above species.

The inoculated cucumber and squash plants developed typical symptoms of western cucumber mosaic, while *N. glutinosa* developed local lesions of tobacco mosaic with the exception of one set of five plants (table 2). After symptoms developed on cucumbers and squash, the virus extract from each of the host plants was inoculated in tomato seedlings and symptoms of western cucumber mosaic appeared on all of them. The cucumber and squash plants had filtered out the tobacco-mosaic virus.

The virus extract from *N. glutinosa* which failed to show local lesions was inoculated in five tomato seedlings which showed positive symptoms of west-

ern cucumber mosaic. It is evident that one of the original tomato plants tested was naturally infected with western cucumber mosaic but not with the tobacco-mosaic virus.

TABLE 2

SEPARATION OF WESTERN-CUCUMBER AND ORDINARY-TOBACCO-MOSAIC VIRUSES IN EXTRACTED JUICE FROM NATURALLY INFECTED TOMATO PLANTS BY MEANS OF FILTER PLANTS

District	Virus extract from tomato plants	Host plants	Number inoculated	Number infected	Type of infection	Symptoms
Byron	Test 1	Cucumber	5	3	Systemic	Mottling
	Test 1	Squash	5	5	Systemic	Cupping, mottling
	Test 1	*Nicotiana glutinosa*	5	3	Local	Local lesions
	Test 2	Cucumber	3	3	Systemic	Mottling
	Test 2	Squash	3	3	Systemic	Cupping, mottling
	Test 2	*N. glutinosa*	3	3	Local	Local lesions
	Test 3	Cucumber	3	1	Systemic	Mottling
	Test 3	Squash	3	3	Systemic	Cupping, mottling
	Test 3	*N. glutinosa*	3	3	Local	Local lesions
Brentwood	Test 4	Cucumber	5	2	Systemic	Mottling
	Test 4	Squash	5	5	Systemic	Cupping, mottling
	Test 4	*N. glutinosa*	5	0	None	None

TABLE 3

MECHANICAL INOCULATION OF HEALTHY TOMATO PLANTS AND EFFECT ON FRUIT WITH VIRUS EXTRACT FROM NATURALLY INFECTED TOMATO FRUIT

District	Virus extract from tomato plants	Host plants	Number inoculated	Number infected	Number malformed fruit	Type of infection	Symptoms
Byron	Test 1	Tomatoes	5	5	2	Systemic	Filiform leaves, western cucumber mosaic
	Test 1	*Nicotiana glutinosa*	5	5	..	Local	Local lesions, tobacco mosaic
	Test 2	Tomatoes	5	5	1	Systemic	Filiform leaves, western cucumber mosaic
	Test 2	*N. glutinosa*	5	5	..	Local	Local lesions, tobacco mosaic
Brentwood	Test 3	Tomatoes	6	6	3	Systemic	Filiform leaves, western cucumber mosaic
	Test 3	*N. glutinosa*	5	5	..	Local	Local lesions, tobacco mosaic

RECOVERY OF VIRUSES FROM NATURALLY INFECTED TOMATO FRUIT

An attempt was made to recover the viruses of western cucumber and tobacco mosaics with the expressed juice of naturally infected fruit and to transmit it to healthy tomato plants by mechanical inoculation, in order to determine the effect on the fruit. Six of 16 inoculated tomato plants developed malformed fruit (table 3).

WESTERN-CUCUMBER-MOSAIC VIRUS

Geographical Distribution. The western-cucumber-mosaic virus occurs in the interior but not in the coastal regions of California. The natural host range includes a large number of economic plants (Severin and Freitag, 1948), ornamental flowering plants, and weeds.

Symptoms on Experimentally Infected Tomato Plants. Juice from Zucchini squash or Golden Self-Blanching celery (*Apium graveolens* var. *dulce*), infected with the western-cucumber-mosaic virus, was used to study the sequence of symptoms on the leaves and the effect on flowers and fruit of tomato. Inoculation experiments were repeated during the spring, summer, and autumn; some years the inoculated plants were kept in cages in the shade or on tables outdoors, in a lathhouse, and in some years in low- and high-temperature greenhouses.

The first symptom of western-cucumber-mosaic virus, usually appearing on the youngest leaves of tomato plants about 14 to 17 days after inoculation at 16° to 19° C, is clearing of the veins and veinlets (plate 4, *A*). The cleared venation cannot be distinguished from that induced by the ordinary-tobacco-mosaic virus. The next symptom is yellow veinbanding (plate 4, *B;* plate 5, *A, B*). The lower and intermediate leaves are curled inward (plate 6), rugose or crinkled with dark-green blister-like elevations (plate 7, *A, B*). About three weeks after inoculation, spear-shaped leaves with spine-like processes (plate 7,*C;* plate 8,*A*) and shoestring or filiform leaflets develop on the apical region of the plants (plate 6). The filiform leaflets are characterized by a marked reduction of the blades often to such an extent that only the midrib and lateral veins are left (plate 7, *D*) or little more (plate 6). About five weeks after inoculation, another type of symptom becomes apparent on the apical portion of the stem, after the filiform leaves are well developed on the intermediate part of the stem. This is the growth of an excessive number of opposite lateral or fern-like leaflets (plate 8, *B*). Frequently fern and filiform leaflets occur on the same compound leaf (plate 9). Later as the infected plants continue to grow large apical leaves develop, the filiform, and fern leaves occurring only on the intermediate portion of the plants. In the advanced stage of the disease, necrosis of the leaves occurs (plate 5, *C*). Infected plants are dwarfed, and the internodes are shortened (plate 6).

The flowers are malformed, turn brown, and become dry adhering to the plant. Doubling and tripling of the fruit (plate 10, *A, B*) can be detected in the flowering stage.

Very little fruit sets. Some of the fruit is malformed, with ridges (plate 11, *A*), furrows, a small fruit telescoped within a large fruit (plate 11, *B*), extreme malformation with development of multiple parts (plate 11, *C*), doubling, tripling, and quadrupling (plate 11, *D*), petals adhering to fruit in ridges (plate 11, *E*), pointed protuberances at blossom end (plate 11, *F*).

Infection by Transplanting Tomato Seedlings. The virus of western cucumber mosaic can be transmitted manually by transplanting tomato seedlings. In one experiment the fingers were submerged into the virus extract from infected tomato plants, and then ten seedlings were transplanted. Six of ten plants developed filiform leaves, a symptom of western cucumber mosaic.

In a second test, the fingers touched the filiform leaves, mottled apical leaves, and stems of infected tomato plants previous to manual transplanting of each of ten tomato seedlings. All plants remained healthy. No tomato plants used as checks or controls were accidentally infected during the past 11 years. The virus is probably spread in pruning, picking, and cultivation operations, as has been reported for the common-cucumber-mosaic virus (Leach, 1940).

Aphid Vectors of Western-Cucumber-Mosaic Virus. Three species of aphids have been proved to be vectors of the western-cucumber-mosaic virus to pansies and violas (Severin, 1947) and to sugar beets (Severin and Freitag, 1948).

The cotton or melon aphid, *Aphis gossypii* Glover, was collected on Honey Dew melons (*Cucumis melo inodorus*) infected with the western-cucumber-mosaic virus near Byron, adjoining the tomato field which showed 95 per cent infection with the same virus. These aphids were transferred from the leaves of Honey Dew melons to healthy tomato plants and *Nicotiana glutinosa*. Sixteen of 22 tomato plants inoculated by the aphids developed filiform leaflets of western cucumber mosaic, but no local lesions of tobacco mosaic appeared on the leaves of *N. glutinosa*. The western-cucumber-mosaic virus could not have been disseminated by the cotton or melon aphid from Honey Dew melons to tomato plants because the disease on tomato plants was widespread before the melons were planted on June 10. Aphids were exceptionally abundant during the spring of 1938 in the northern San Joaquin Valley.

During 1939 surveys were made of the tomato fields in the Byron and Brentwood districts. The population of aphids was low during the spring of 1939. An examination of tomato seedbeds showed the presence of a very small number of aphids. No symptoms of the multiple viruses of western cucumber and tobacco mosaics were detected on any tomato plant during the 1939 growing season.

Efforts to colonize species of aphids on tomato plants in the greenhouse have met with varying success. It was noted that many species of aphids seem unable to maintain themselves on tomato plants, possibly because the plant exudate adheres to the tarsi and holds them fast. The lily aphid, *Myzus circumflexus* (Buckton), and the foxglove aphid, *M. solani* (Kaltenbach), reproduced but neither of these species are efficient vectors of the western-cucumber-mosaic virus to tomato plants. The green peach aphid, *Myzus persicae* (Sulzer), has been found on tomato plants under natural conditions. The following species of aphids failed to multiply on tomatoes.

Celery aphid, *Aphis apii* Theobald[4]
Rusty-banded aphid, *Aphis ferruginea-striata* Essig
Cotton or melon aphid, *Aphis gossypii* Glover
Bean or dock aphid, *Aphis rumicis* L.
Cabbage aphid, *Brevicoryne brassicae* L.
Yellow willow aphid, *Cavariella aegopodii* (Scopoli)
Pea aphid, *Macrosiphum pisi* (Kaltenbach)
Ornate aphid, *Myzus ornatus* Laing
Honeysuckle aphid, *Rhopalosiphum conii* (Hottes)
Turnip or false cabbage aphid, *Rhopalosiphum pseudobrassicae* (Davis)

[4] According to E. O. Essig (personal interview) *Aphis apii* Theobald may be identical with *A. helianthi* Monell.

Certain species of aphids are capable of transmitting the virus of western cucumber mosaic to tomatoes. In addition to the cotton aphid or melon aphid, the lily aphid and the green peach aphid transmit the virus on rare occasions to tomato plants.

TOMATO- OR ORDINARY-TOBACCO-MOSAIC SYMPTOMS ON EXPERIMENTALLY INFECTED TOMATO PLANTS

From the literature it appears that the virus causing tomato mosaic is identical with the ordinary-tobacco-mosaic virus. The first symptom is cleared veins and veinlets (plate 12, *A*) appearing on the younger leaves about one week after inoculation. The early stage of the disease is marked by stunting of the whole plant and by folding or rolling of the leaves along the midribs. The leaflets flatten out and the normally rounded lobes become spear-shaped with spine-like projections (plate 14, *C*). The smaller leaflets may be reduced to filiform (plate 13, *A*) or fern leaf (plate 13, *B*) structures, or both may occur on the same leaf. In the next stage, dark-green blister-like elevations (plates 12, 14, *B*) appear on the upper surface of some of the leaflets. Later pale-green or yellow areas or a diffuse mottling (plate 15) appear between the veins of the leaflets.

The fruit on tomato plants infected with the ordinary-tobacco-mosaic virus is rarely malformed and no extreme transformations occur. On rare occasions tomato fruit may show furrows (plate 16, *A*), or ridges (plate 16, *B*). The symptoms on the two fruits illustrated were the most severe ever encountered. Moreover it is doubtful whether these malformations of tomato fruit were the result of tobacco-mosaic virus infection, since these deformations also occur, on rare occasions, on tomato fruit of healthy plants, especially at the end of the growing season, when the leaves turn brown and dry.

MULTIPLE VIRUSES OF CELERY CALICO AND ORDINARY TOBACCO MOSAIC

Tomato plants were demonstrated to be naturally infected with the viruses of celery calico and tobacco mosaic at Berkeley during 1949. In the spring many tomato plants showed leaf symptoms of celery calico. The virus extract from the infected plants was inoculated in healthy tomato plants, sugar beets (*Beta vulgaris*), White Spine cucumbers (*Cucumis sativus*), Zucchini squash (*Cucurbita pepo*), and *Nicotiana glutinosa*. Typical symptoms of calico developed on beets (Severin and Freitag, 1948), cucumber (Severin, 1942), and squash. No local lesions appeared on *N. glutinosa*, indicating that the tomato plants were free of the tobacco-mosaic virus. During the autumn, however, when the same species of host plants were inoculated with the expressed juice of tomato plants infected with the multiple viruses, symptoms of calico appeared on the leaves of beets, cucumbers, and squash, and local lesions of tobacco mosaic appeared on *N. glutinosa*.

When tomato plants infected with calico were inoculated with the tobacco-mosaic virus, numerous filiform leaves developed; the plants were stunted and bore little fruit. Such fruit as did develop showed furrows (plate 17, *A, B*); ridges, doubling (plate 17, *C*); tripling; quadrupling; and other

extreme malformations, some fruit pointed at the apex, some rounded or blunt (plate 17, *D, E, F*).

There are no symptoms on tomato plants which are reliable in distinguishing multiple virus infection of celery calico and tobacco mosaic from those of western cucumber and tobacco mosaics.

MULTIPLE VIRUSES OF COMMON CUCUMBER AND ORDINARY TOBACCO MOSAICS

When tomato plants infected with common-cucumber-mosaic virus are inoculated with tobacco-mosaic virus, the symptoms induced on the fruit are less severe than with either the multiple viruses of western cucumber and tobacco mosaics or the virus complex of celery calico and tobacco mosaic. Some of the fruit on tomato plants infected with the common-cucumber and tobacco-mosaic viruses may show furrows (plate 18, *B, C, E*), ridges (plate 18, *D*), and indentations (plate 18, *F*).

Symptoms Distinguishing Tomato Plants Infected with the Common-Cucumber-Mosaic Virus from Those Infected with the Tobacco-Mosaic Virus. According to Mogendorf (1930) it is usually not difficult to distinguish between filiform leaves of a common-cucumber-mosaic-infected tomato plant and the malformed leaves of a tobacco-mosaic-infected plant of the same age. The filiform leaves show decidedly fewer dark-green blister-like elevations, or none at all, and they do not stand out so rigidly but rather hang down flaccidly or curl around like tendrils. The mottling produced by the common-cucumber-mosaic virus yields larger dark- and pale-green areas, in contrast to the delicate mosaic pattern of minute, sharply defined, angular spots of two shades of green (intensified green usually being absent) induced by the tobacco-mosaic virus.

COMMON-CUCUMBER-MOSAIC VIRUS

Geographical Distribution. Common cucumber mosaic is a destructive disease of cucumber and other host plants in the middlewestern and eastern United States, but has not been known to occur in California up to the present time.

Symptoms on Experimentally Infected Tomato Plants. Mogendorf (1930) has given a detailed description of the symptoms of the tomato disease caused by mechanical inoculation with the common-cucumber-mosaic virus.

SUMMARY

During 1938 a serious outbreak of multiple virus infection, involving western cucumber mosaic and ordinary tobacco mosaic, occurred in the northern San Joaquin Valley, California.

The symptoms induced by these multiple viruses on the foliage, flowers, and fruit of tomato plants (*Lycopersicon esculentum*) are described, as well as the symptoms produced by the separated viruses on the leaves. The virus complex causes abnormal flowers, and such severe deformation of the fruit as ridges, furrows, doubling, tripling, quadrupling and other extreme malformations.

The multiple viruses were separated by heating the virus extract to 83° C, thus inactivating the western-cucumber-mosaic virus at 65° C, but allowing the tobacco-mosaic virus to remain active (thermal inactivation 90°–95° C). The virus complex was also separated by means of inoculating filter plants susceptible to only one of the viruses.

The symptoms induced by another virus complex in tomato, consisting of celery calico and tobacco mosaics, are also described. This combination of viruses causes furrows, doubling, and extreme malformations of the fruit. There are no reliable symptoms which are useful in distinguishing multiple virus infection of celery calico and tobacco mosaic from western cucumber and tobacco mosaics on tomato plants.

The virus complex of common or eastern and middlewestern cucumber and tobacco mosaics induces similar but less severe fruit malformation than that resulting from virus complexes of western cucumber and tobacco mosaic, or of western cucumber and tobacco mosaic.

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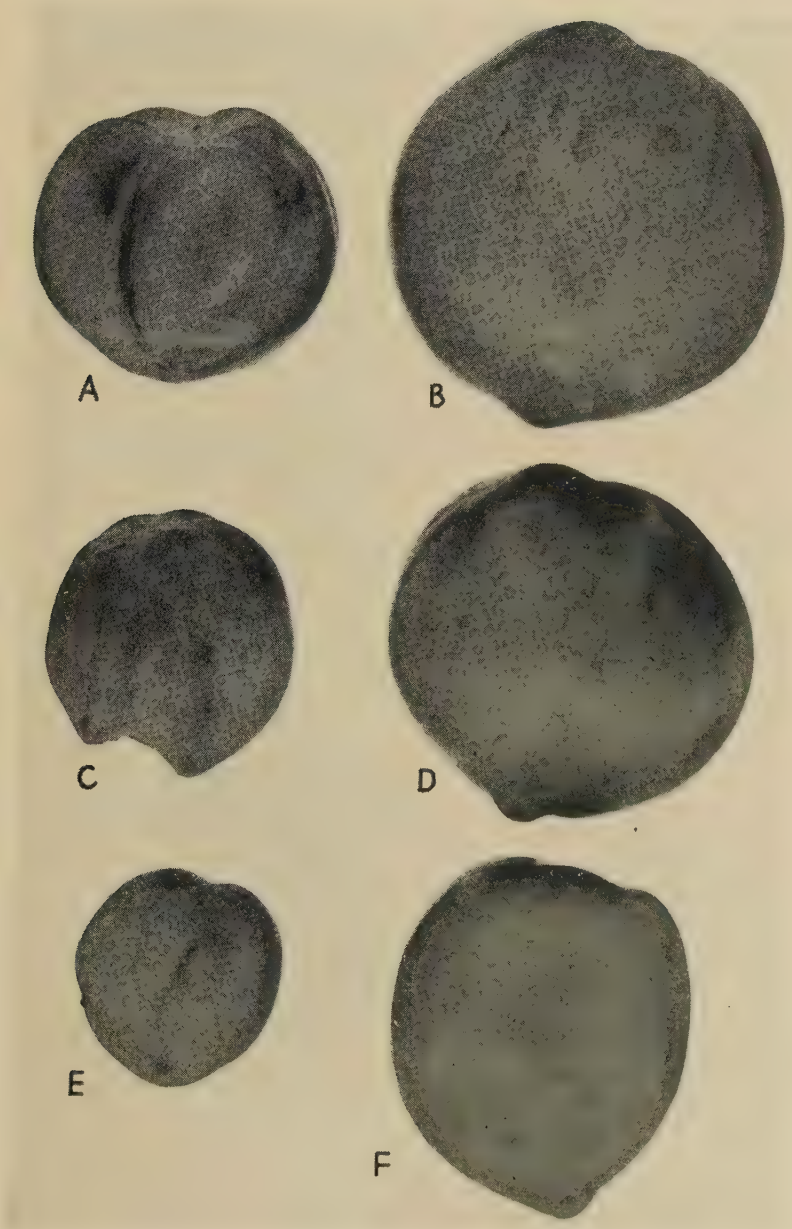

Plate 1. Symptoms of multiple viruses of western cucumber and ordinary tobacco mosaics on fruit of naturally infected tomato plants (*Lycopersicon esculentum*) showing pointed protuberances (*A–F*) at blossom end (Brentwood, 24 October 1938).

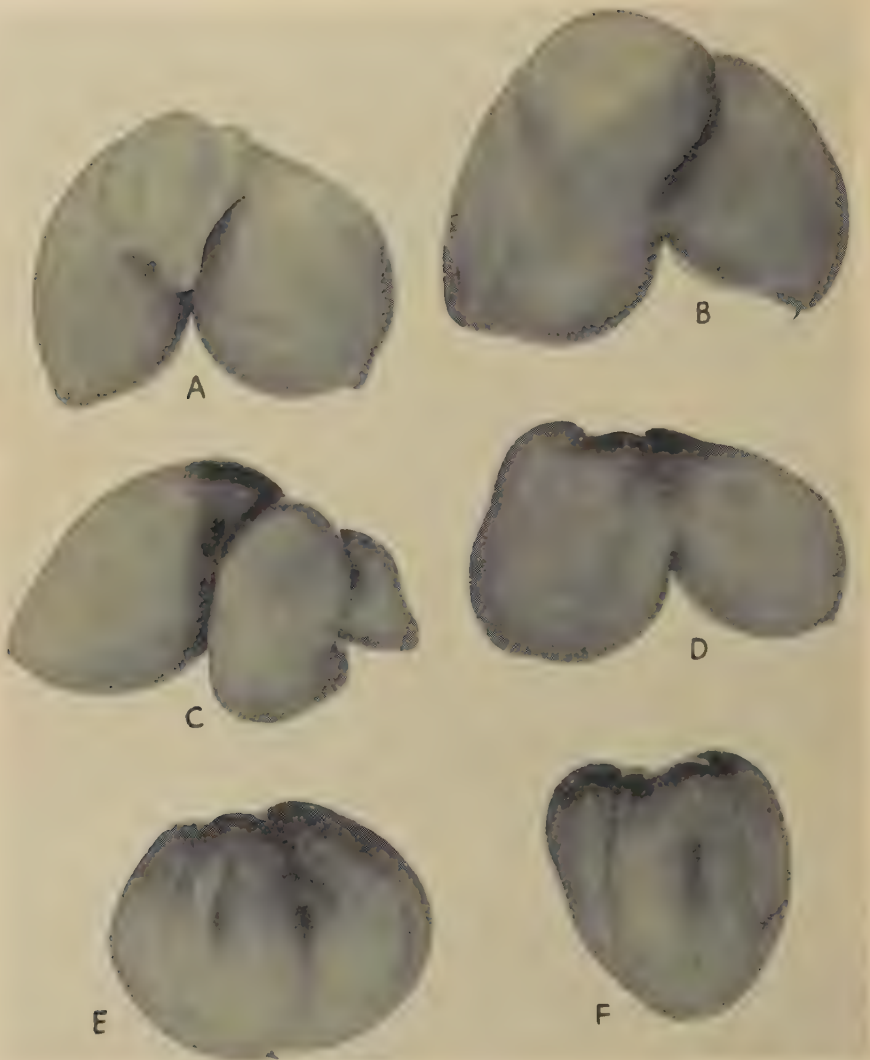

Plate 2. Symptoms of multiple viruses of western cucumber and ordinary tobacco mosaics on fruit from naturally infected tomato plants (*Lycopersicon esculentum*): *A*, *B*, *C*, tripling; *D*, doubling; *E*, furrows; *F*, furrows and pointed protuberance at blossom end (Brentwood, 24 October 1938).

Plate 3. Symptoms of multiple viruses of western cucumber and ordinary tobacco mosaics on fruit from naturally infected tomato plants (*Lycopersicon esculentum*): *A*, ridge; *B*, projection; *C*, protuberances; *D*, doubling; *E*, two small fruits telescoped in a large fruit; *F*, ridges and protuberances at blossom end (Riverside, 2 November 1938).

Plate 4. Symptoms of western-cucumber mosaic virus on the leaves of mechanically inoculated Marglobe tomato plants (*Lycopersicon esculentum*): *A*, cleared veins and veinlets; *B*, cleared veinlets, yellow veinbanding, and early stage of mottling.

Plate 5. Symptoms of western-cucumber-mosaic virus on leaves of mechanically inoculated Marglobe tomato plants (*Lycopersicon esculentum*): *A*, yellow veinbanding and yellow and deep-green coarse mottle (also shown in *B*); *C*, necrosis of leaflet.

Plate 6. Symptoms of western cucumber mosaic virus on experimentally infected entire Marglobe tomato plant (*Lycopersicon esculentum*) showing inward-curled lower and intermediate leaves and shoestring or filiform apical leaves. The infected plant is dwarfed, internodes shortened, giving the plant a bushy, compact, upright habit of growth.

Plate 7. Symptoms of western-cucumber-mosaic virus on leaves of mechanically inoculated Marglobe tomato plants (*Lycopersicon esculentum*): *A*, *B*, blisterlike elevations; *C*, spear-shaped leaflets; *D*, filiform leaflets reduced to midrib and lateral veins.

Plate 8. Symptoms of western cucumber mosaic virus on leaves of mechanically inoculated Marglobe tomato plants (*Lycopersicon esculentum*): left, spear shaped leaflets with spine-like processes; right, excessive number of lateral or fern-shaped leaflets.

Plate 9. Symptoms of western-cucumber-mosaic virus on leaf of mechanically inoculated Marglobe tomato plant (*Lycopersicon esculentum*) showing fern and filiform leaflets on the same compound leaf.

Plate 10. Symptoms of western-cucumber-mosaic virus on flowers of mechanically inoculated Marglobe tomato plants (*Lycopersicon esculentum*): *A*, doubling, and *B*, tripling of fruit.

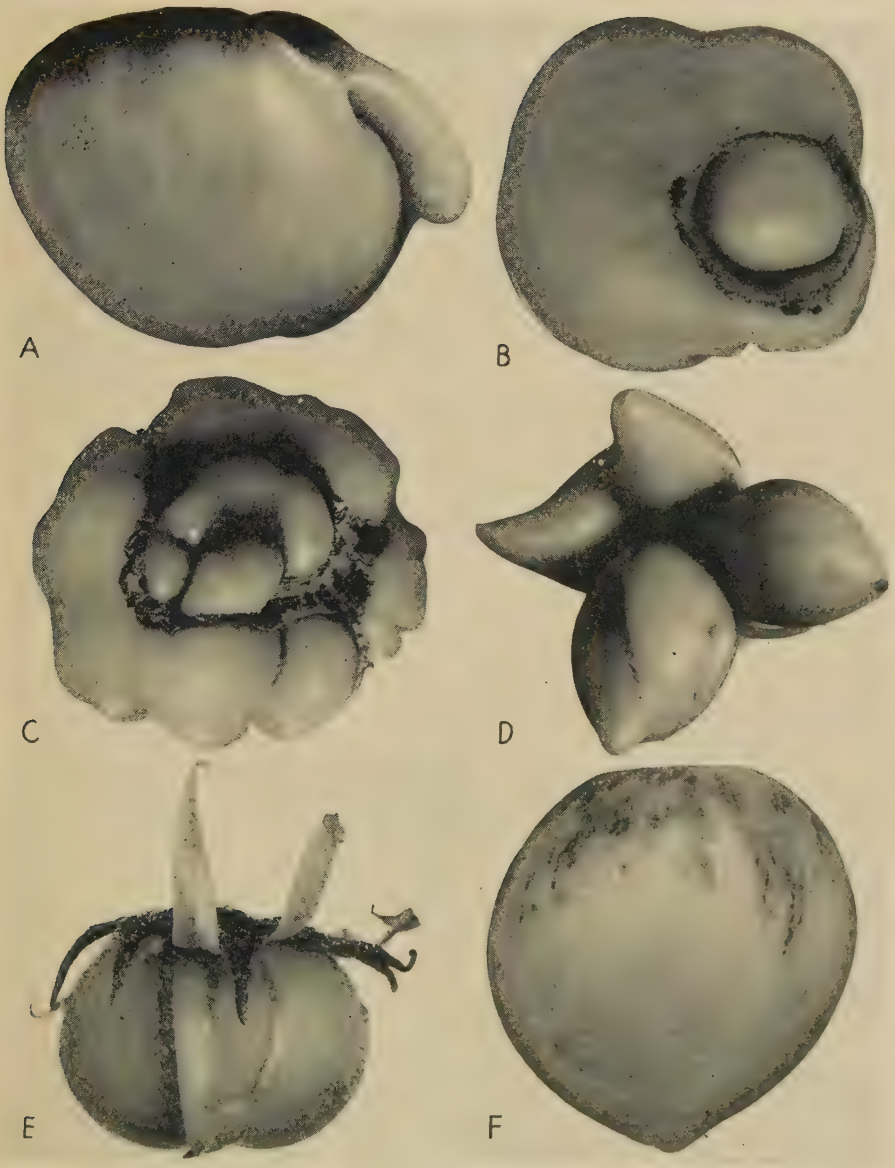

Plate 11. Symptoms of western cucumber-mosaic virus on fruit of mechanically inoculated Marglobe tomato plants (*Lycopersicon esculentum*): *A*, ridge-like protuberance; *B*, a small tomato teleseoped within a large tomato; *C*, extreme malformation of fruit with development of multiple parts; *D*, quadrupling; *E*, petal attached to tomato forming ridge; *F*, pointed protuberance at blossom end.

Plate 12. Symptoms of ordinary-tobacco-mosaic virus on leaves of mechanically inoculated Marglobe tomato plants (*Lycopersicon esculentum*) at low temperatures: *A*, cleared veins and veinlets; *B*, dark-green, blisterlike elevations on the upper surface of some of the leaflets.

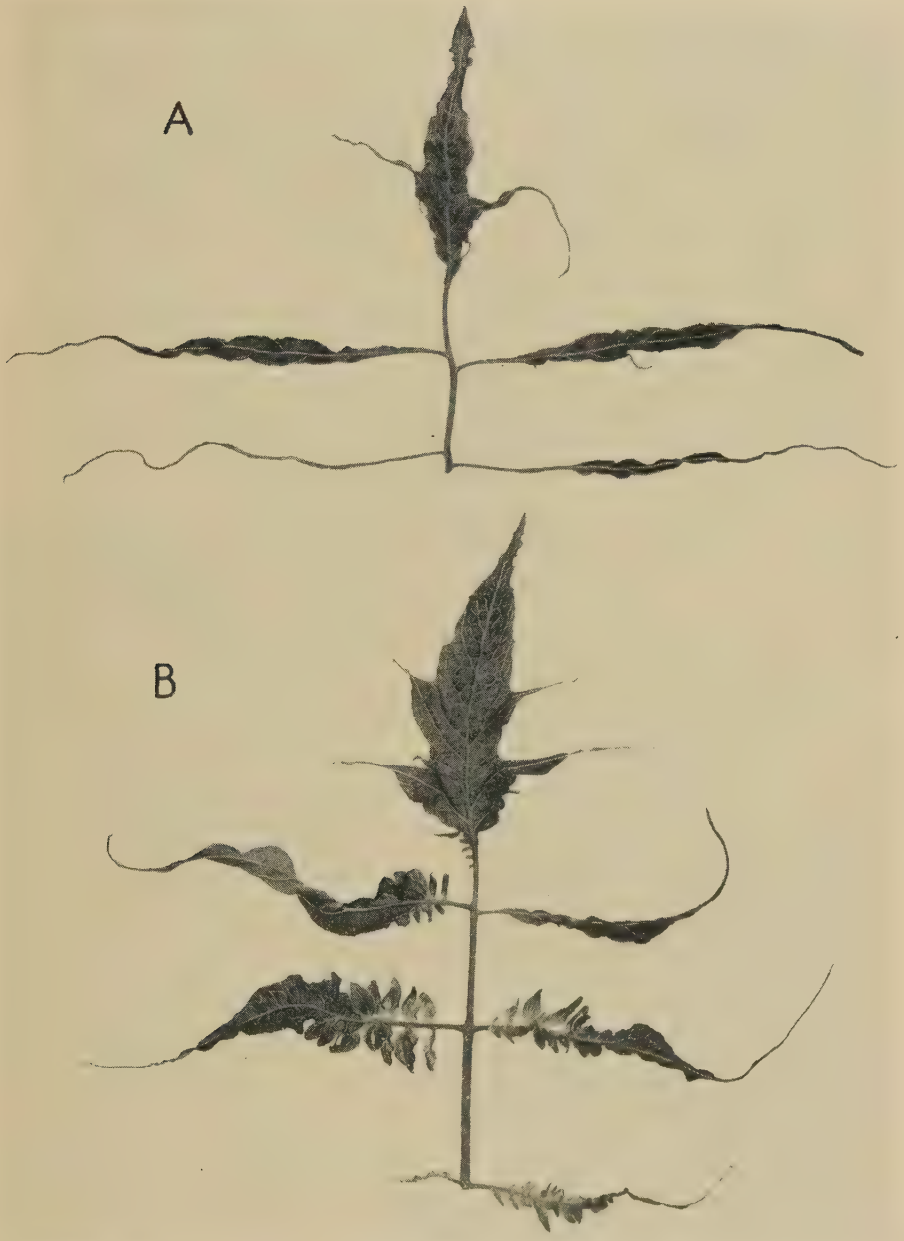

Plate 13. Symptoms of ordinary-tobacco-mosaic virus on leaves of mechanically inoculated Marglobe tomato plants (*Lycopersicon esculentum*) at low temperatures: *A*, spear-shaped leaflets with spine like processes, lower left, filiform leaflets; *B*, spear shaped apical leaflets with spine-like processes and fern-like leaflets.

Plate 14. Symptoms of ordinary-tobacco-mosaic virus on leaves of mechanically inoculated Marglobe tomato plants (*Lycopersicon esculentum*) at low temperatures: upper left, faint mottling; lower left, blisterlike elevation; right, spear-shaped leaflets with spine-like processes.

Plate 15. Symptoms of ordinary tobacco mosaic virus on leaves of mechanically inoculated Marglobe tomato plants (*Lycopersicon esculentum*) showing pale green or yellow areas, or diffuse mottling, on fern-like leaflets.

Plate 16. Symptoms of ordinary tobacco-mosaic virus on fruit of mechanically inoculated Marglobe tomato plants (*Lycopersicum esculentum*). *A*, furrows; *B*, ridges. It is doubtful whether these malformations were the result of tobacco-mosaic virus infection, since these deformations also occur on rare occasions on tomato fruit of healthy plants.

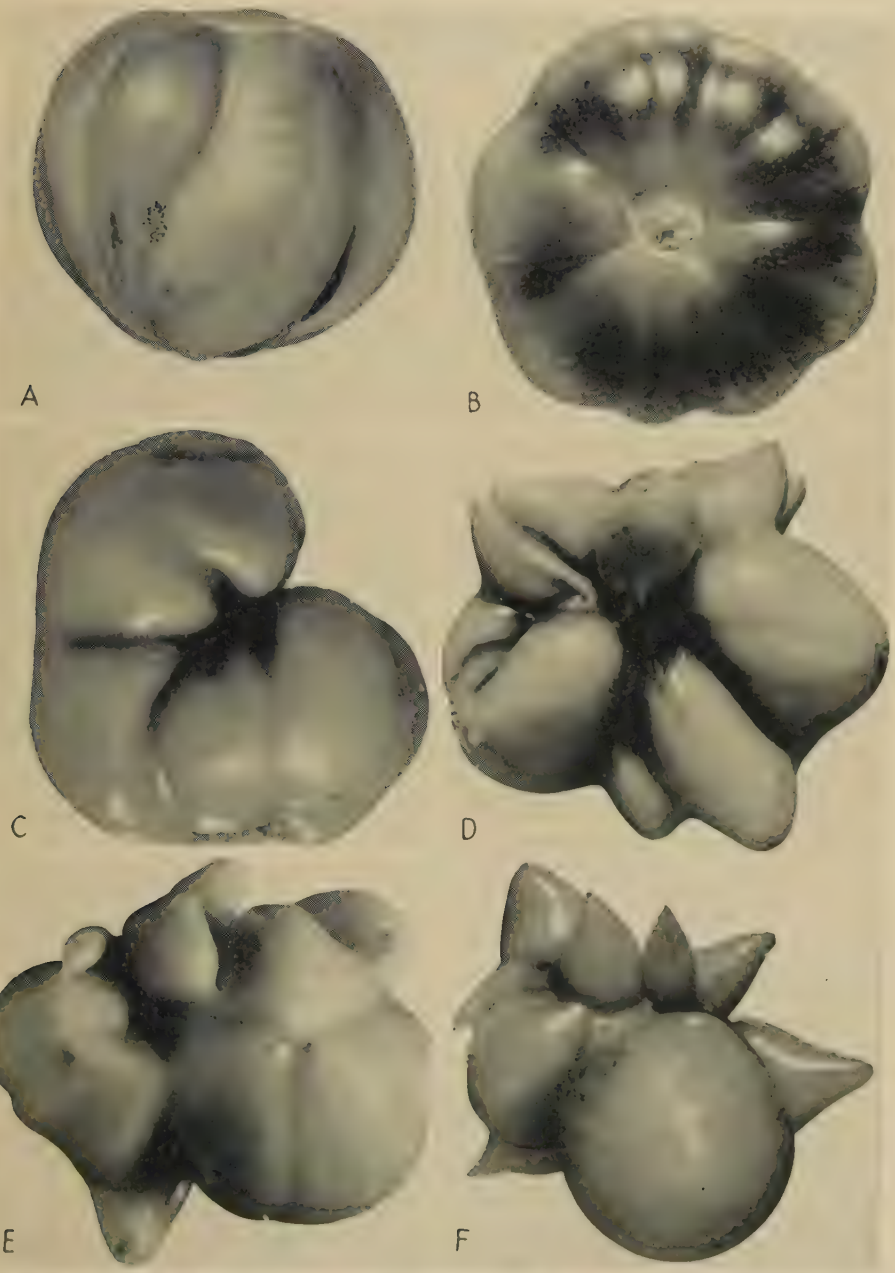

Plate 17. Symptoms of multiple viruses consisting of celery-calico and tobacco-mosaic viruses on fruit of mechanically inoculated Marglobe tomato plants (*Lycopersicon esculentum*): *A, B*, furrows; *C*, doubling; *D, E, F*, multiple segments of fruit, some pointed at apex and some rounded or blunt.

Plate 18. Symptoms of multiple viruses consisting of common cucumber and ordinary tobacco mosaics on fruit of mechanically inoculated Marglobe tomato plants (*Lycopersicon esculentum*): *A*, fruit from healthy check or control plant; *B*, *C*, ridges with shallow furrows; *D*, ridges; *E*, tripling; *F*, indentations.

SYMPTOMS OF THE CELERY-CALICO VIRUS ON TOMATO PLANTS[1]

HENRY H. P. SEVERIN

DURING THE SPRING of 1949 tomato plants naturally infected with the celery-calico virus were common at Berkeley, Alameda County, but during the autumn some of the plants developed symptoms of spotted wilt consisting of a bronzing of the leaflets (plate 1) which killed the leaves outright (plate 2).

The symptoms of the tomato spotted-wilt virus on the fruit were pale-yellow areas in the normal green skin (plate 3, *A*), pale-red areas embedded in white areas (plate 3, *D*), pale-red, circular areas surrounded by yellow and dark rings (plate 3, *E*), and numerous pale-red, circular areas, each surrounded by a white ring embedded in the normal red skin of a ripe tomato (plate 3, *F*).

In this paper are described the geographical distribution and the symptoms of the celery-calico virus produced on the leaves and fruit of tomato plants of the Marglobe variety. Symptoms on tomato plants induced by the celery-calico virus are compared with those caused by the western-cucumber-mosaic virus, described in the preceding paper (Severin, 1950), in order to differentiate these two diseases.

MATERIALS AND METHODS

The original source of the celery-calico virus was naturally infected celery obtained near Milpitas in the Santa Clara Valley. The carborundum method of inoculation described by Rawlins and Tompkins (1936) was used.

CELERY-CALICO VIRUS

Geographical Distribution. The celery-calico virus is a strain of a cucumber-mosaic virus. It is common in the coastal fog belt and also occurs in the hot interior regions of California. Celery calico has been found in all of the large celery districts of the state (Severin and Freitag, 1938). The geographical distribution of the celery-calico virus includes California, Washington, and Idaho (Severin, 1942).

Symptoms on Leaves of Mechanically Inoculated Tomato Plants. The first symptom of the celery-calico virus two weeks after inoculation of tomato plants is cleared veinlets on the inoculated leaves (plate 4, *A*). The lower leaves develop small to large, dark-green, circular areas (plate 4, *C*) and later, on the intermediate leaves, chlorotic areas (plate 5, *A*), followed by green blisterlike elevations (plate 4, *B*) accompanied by distortion of the leaflets (plate 6). In old plants a lemon-yellow or orange discoloration appears on a portion of each leaflet (plate 7) and spreads until the entire leaf is affected. A progressive orange discoloration of the lower leaves of the main stem and lateral branches occurs, but the younger leaves remain green. This symptom of calico may be readily overlooked, since a natural yellowing of the lower leaves occurs on healthy check or control plants, especially on old

[1] Received for publication October 20, 1949.

plants. Near the apical end of the stem, the midribs bend downward and the leaflets are cupped inward. A slight yellowing of the youngest leaflets occurs. In the advanced stage of the disease, necrosis of the leaflets occurs (plate 5, *B, C*).

These symptoms developed in a low-temperature greenhouse at 16° to 19° C. The infected plants were not stunted, growing four to five feet tall, and bearing an abundance of normal fruit.

The absence of filiform and fern leaf symptoms with the celery-calico virus differentiates this disease from that produced by the western cucumber mosaic described in the companion paper (Severin, 1950).

APHID VECTORS

Nine species of aphids have been reported to transmit the celery-calico virus to perennial delphiniums (Severin, 1942) and 11 aphid species to pansies and violas (Severin, 1947).

SUMMARY

The sequence of symptoms of the celery-calico virus on the leaves of tomato plants of the Marglobe variety (*Lycopersicon esculentum*) is cleared veins and veinlets on the inoculated leaves; small to large dark-green, circular areas and later chlorotic areas on the intermediate leaves; green blisterlike elevations accompanied by the distortion of the leaflets, and a lemon-yellow or orange discoloration of the lower leaves.

The absence of filiform-leaf and fern-leaf symptoms with the celery-calico virus differentiates this disease from that produced at low temperatures by the western-cucumber-mosaic virus described in the companion paper (Severin, 1950).

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Plate 1. Symptoms of tomato-spotted wilt virus on leaf of naturally infected tomato plant (*Lycopersicon esculentum*) showing characteristic bronzing of the leaflets.

Plate 2. Symptoms of tomato-spotted-wilt virus on naturally infected tomato seedling (*Lycopersicon esculentum*) showing leaves killed outright by bronzing.

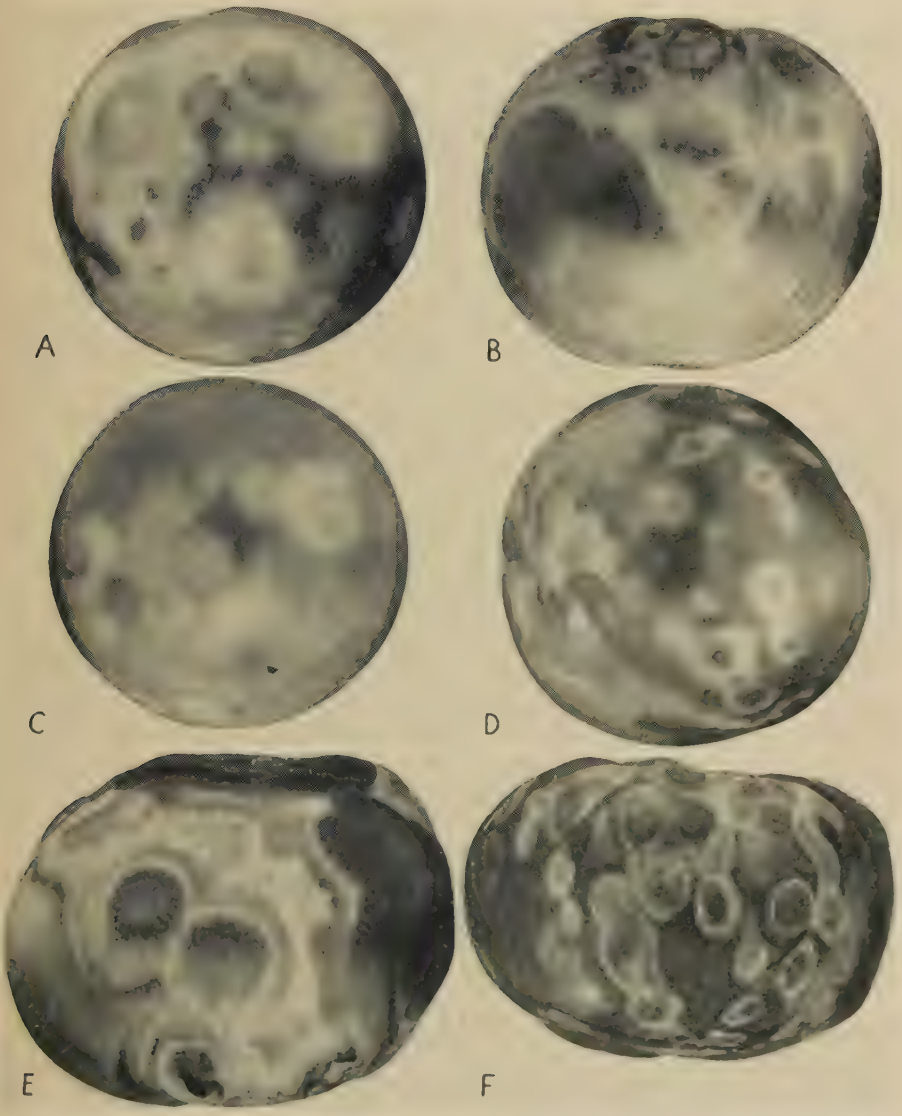

Plate 3. Symptoms of tomato-spotted-wilt virus on fruit of naturally infected tomato plants (*Lycopersicon esculentum*). *A*, pale yellow areas in normal green skin; *B*, pale red areas in the normal green skin; *C*, concentric circles; *D*, pale red areas embedded in white areas; *E*, pale red, circular areas surrounded by yellow and dark rings; *F*, numerous pale red, circular areas each surrounded by a white ring embedded in the normal red skin of a ripe tomato.

Plate 4. Symptoms of celery-calico virus on leaves of mechanically inoculated Marglobe tomato plants (*Lycopersicon esculentum*): *A*, cleared veinlets; *B*, blisterlike elevations; *C*, small to large, dark-green, circular areas.

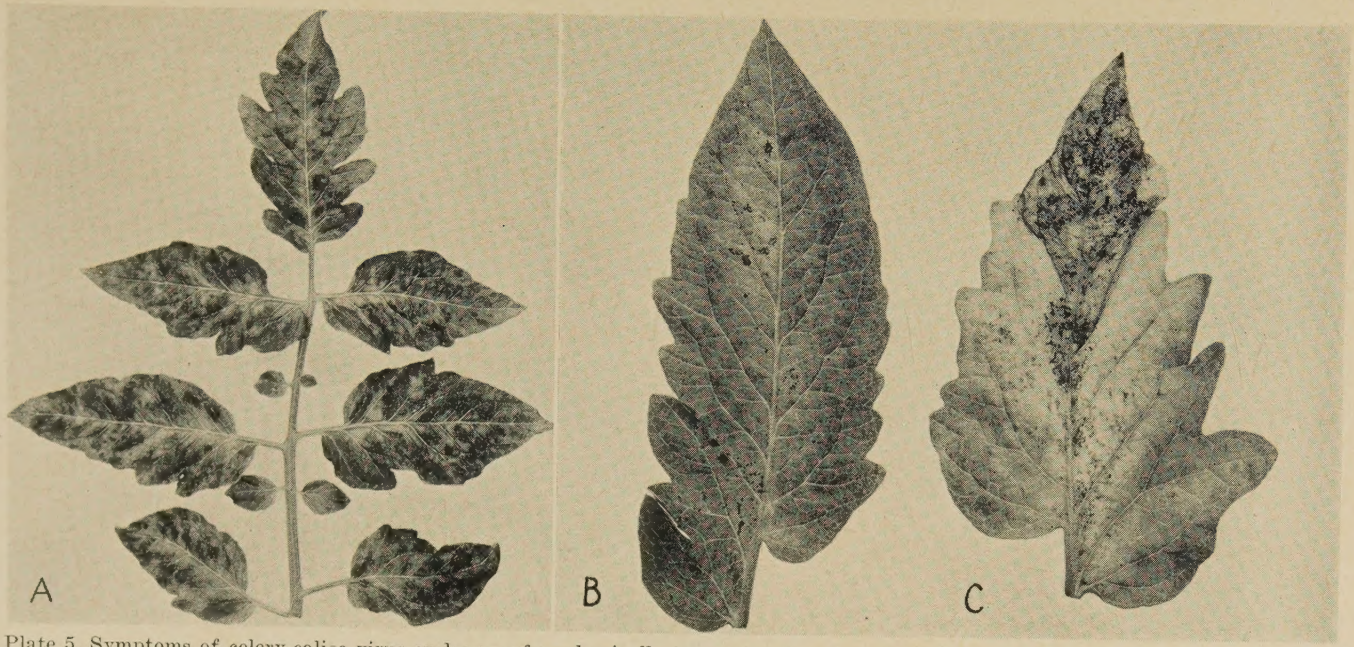

Plate 5. Symptoms of celery-calico virus on leaves of mechanically inoculated Marglobe tomato plants (*Lycopersicon esculentum*): *A*, chlorotic areas on intermediate leaf; *B*, *C*, necrosis of leaflets.

Plate 6. Symptoms of celery-calico virus on leaf of mechanically inoculated Marglobe tomato plant (*Lycopersicon esculentum*) showing green blisterlike elevation and distorted leaflets.

Plate 7. Symptom of celery-calico virus on leaflets of mechanically inoculated Marglobe tomato plant (*Lycopersicon esculentum*) showing orange discoloration.